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GREENHOUSE EXPERIMENTS ON THE RUST RESISTANCE OF OAT VARIETIES.[1]

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INTRODUCTION.

The rusts have long been recognized as one of the most serious limiting factors in the production of wheat and oats, both in the United States and in other countries. Considerable work has been done on the problem of controlling rust in wheat through resistant varieties and some results have been published, but very little specific information has been made available on the rust resistance of oat varieties in the United States.

The importance of the oat crop among the small grains in the United States is second only to that of wheat, and the problem of rust control is perhaps even more acute, for oats are more widely grown in localities favorable to rusts. For this reason a proper choice of varieties, based on accurate experimental tests, is a necessary factor in successful oat culture. The present paper presents the results obtained in greenhouse culture work with the crown rust of oats, *Puccinia lolii avenae* McAlpine (Pl. I, fig. 2, and Pl. II), and

[1] The work here described was a part of the graduate studies of the writer during the college year 1915–16 at Cornell University and was a continuation of investigations conducted for several years while in the United States Department of Agriculture. The departments of plant breeding and plant pathology in the university provided every facility for the work, which was carried out under the supervision of Dr. H. H. Love, to whom thanks are due for many helpful suggestions.

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the stem rust of oats, *Puccinia graminis avenae* Erikss. and Henn. (Pl. I, fig. 1, and Pl. III). These rusts are both rather common in the United States. The stem rust probably causes the greater loss in the Northern States and the crown rust in the Southern States.

THE CULTURE OF CEREAL RUSTS IN THE GREENHOUSE.

Obligate parasitism is a well-known characteristic of the rust fungi, and all attempts to grow them in artificial media have failed. They are easily cultured on the living host, however, and, as pointed out by Carleton (2),[1] it is possible to make many interesting studies by this method. Carleton described the method of inoculation used by him and gave suggestions concerning work with rusts.

Evans (4) has tested the rust resistance of oat varieties in the greenhouse and concludes that the Indian varieties are far more susceptible to the crown rust than to the stem rust.

Melhus (8) has described and illustrated the apparatus used and has given his methods in culturing parasitic fungi on the living host, including notes on culture work with the crown rust of oats.

Fromme (5) has published a comprehensive paper dealing with the culture of cereal rusts in the greenhouse, in which he briefly reviews the work of previous writers and describes in some detail his own methods, particularly the results obtained with the crown rust of oats.

Stakman (12) briefly describes culture methods used in his greenhouse studies of biologic forms of the cereal rusts and calls attention to the effects of temperature, humidity, and light on the incubation period. In a second paper (13) he has briefly described similar methods used in the additional study of cereal rusts on plants grown in the greenhouse.

Melchers (7) has suggested the use of galvanized-iron tubs with window-glass covers as moist chambers. He also advocates wetting the leaves to be inoculated by the "finger-rubbing" method instead of with an atomizer and keeping the pots bearing the rusted leaves in shallow pans of water, to avoid the necessity of overhead watering.

EXPERIMENTAL METHODS.

In the greenhouse experiments of the writer, methods similar to those above cited were employed. For the infection studies on seedling oat plants 4-inch pots were used, and 5-inch pots for the plants inoculated at heading time. Greenhouse potting soil of approximately the same make-up was used throughout the work. For the studies of plants at heading time four seeds of a variety were sown in each pot. When the plants were 6 to 8 inches high they were thinned to two in a pot, the number usually reserved for subsequent inoculation.

[1] The serial numbers in parentheses refer to "Literature cited," p. 16.

FIG. 1.—STEM RUST OF OATS: UREDINIA ON LEAVES, TELIA ON STEM.

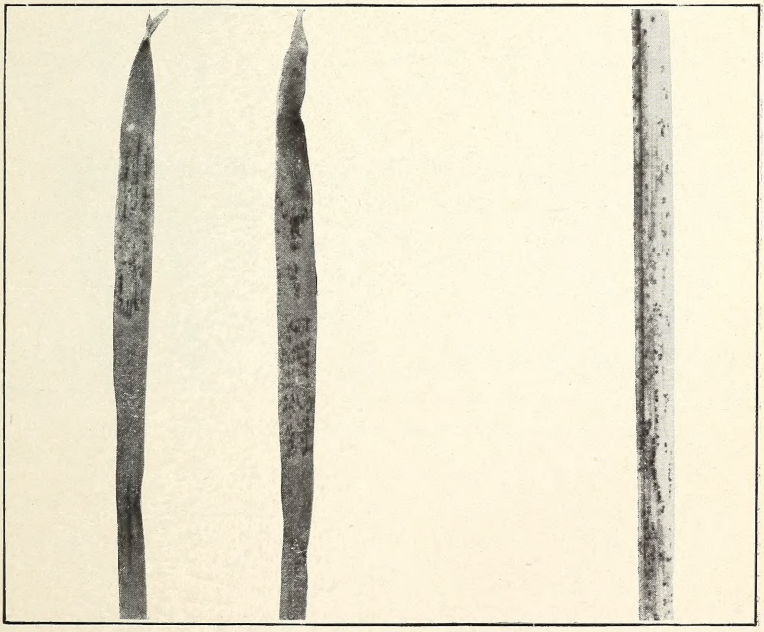


FIG. 2.—CROWN RUST OF OATS: UREDINIA ON LEAVES, TELIA ON STEM.

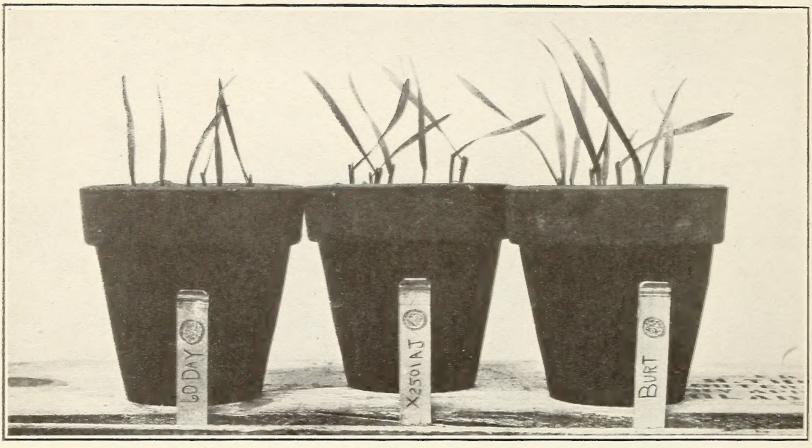


FIG. 1.—SEEDLING OAT PLANTS INOCULATED WITH CROWN RUST.

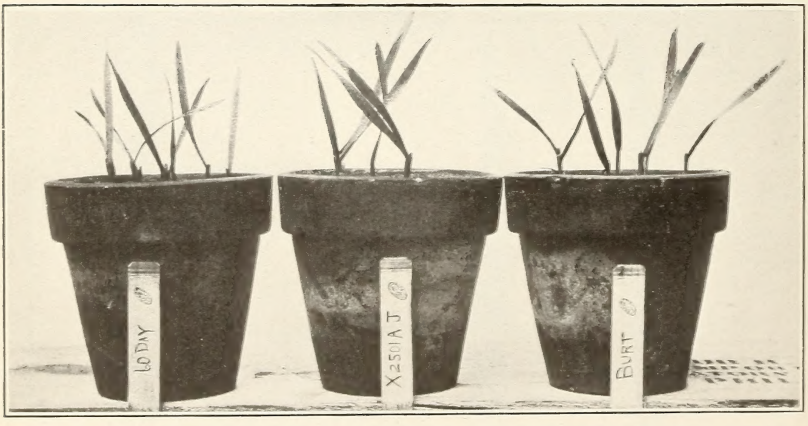
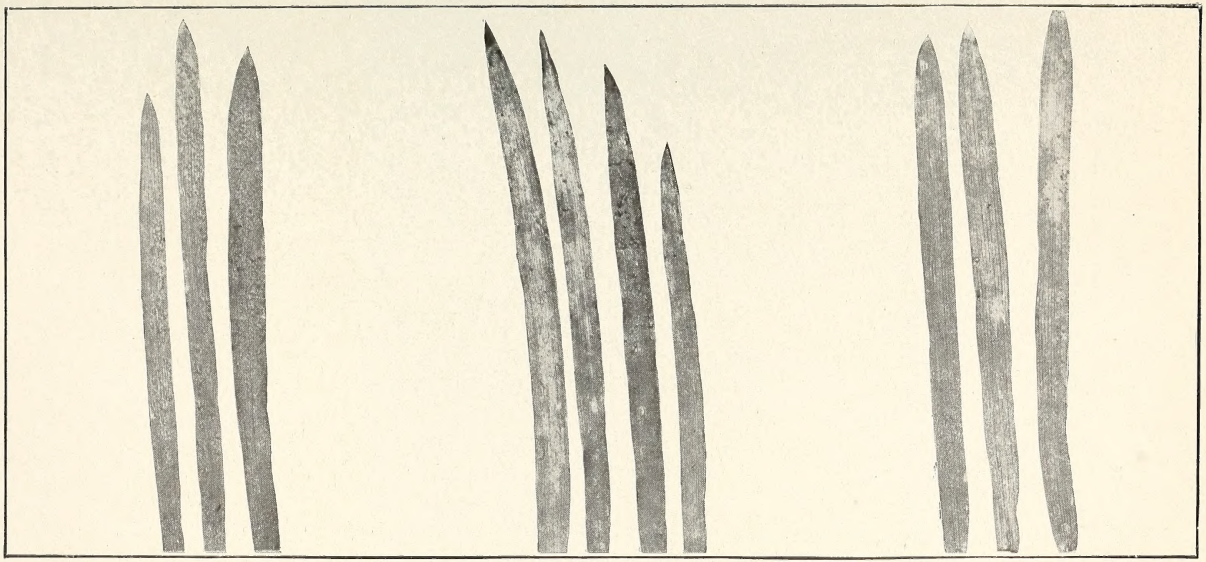


FIG. 2.—SEEDLING OAT PLANTS INOCULATED WITH STEM RUST.



SEEDLING LEAVES OF TWO STRAINS OF BURT OATS INFECTED WITH CROWN RUST, SHOWING ONLY A FEW SMALL PUSTULES BUT MANY FLECKS.

About 15 seeds per pot were sown for the seedling work, and the plants were thinned later, so that on an average about 8 plants per pot were inoculated. Plantings were made every few days from November, 1915, to April, 1916. Thus, there was always a series of plants coming on; as soon as one series had been inoculated another was about ready.

The cultures were kept in a cool greenhouse (night temperature, 50° to 55° F.; day temperature, 60° to 65° F.) and watered not less often than every alternate day. The inoculations on the seedling

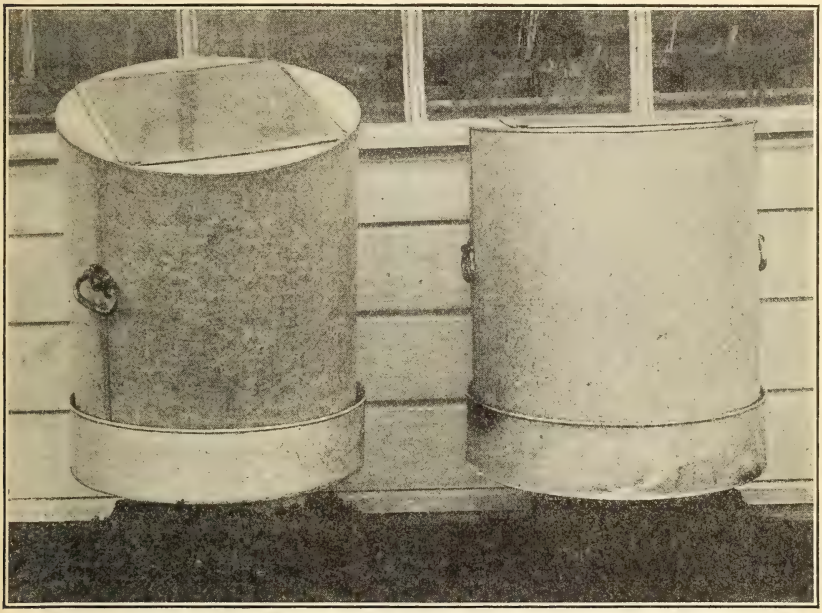


FIG. 1.—Glass-topped galvanized-iron moist chamber used for seedling plants.

plants were always made when the first (seedling) leaf was still vigorous and of a normal green color; that is, when the plants were only 3 to 5 inches high. This first leaf was always the only one inoculated. All others, with the "shoot," were kept trimmed off.

Spore material of both the oat rusts was obtained from the Minnesota Agricultural Experiment Station and increased for use as needed on stock cultures of the White Tartarian oat, the variety used as a check.

About ten varieties usually constituted the series treated on any one day, one set being inoculated with stem rust and the other with crown rust. No plants were left uninoculated, but one pot of White Tartarian serving as a check on the other varieties was always sown and inoculated with each series.

The inoculations were made by removing urediniospores with a flattened needle from a leaf bearing a heavy infection and placing

them on the previously moistened leaf to be inoculated. When all leaves in a pot were inoculated they were sprayed at once with an atomizer and placed in the moist chamber shown in figure 1, where they were allowed to remain 48 hours. These moist chambers, which will hold about forty 4-inch pots, cost less than $10 for four. No trouble was experienced from the leaves burning or turning yellow, and almost 100 per cent of the inoculations were successful.

Inoculations of older plants were made in the order of heading of the varieties, beginning on April 10 and continuing to May 9, 1916. There were 12 to 18 plants in each series. The stem-rust spores were always placed on the sheath inclosing the emerging panicle, while the inoculations with crown rust were made on the uppermost leaf blade. As with the seedlings, the inoculated plants were sprayed with an atomizer to insure the presence of a film of water and then kept in the moist chamber for two days. A special large glass-topped galvanized-iron moist chamber was made, holding eighteen 5-inch pots and allowing the tallest plants to remain upright (fig. 2).

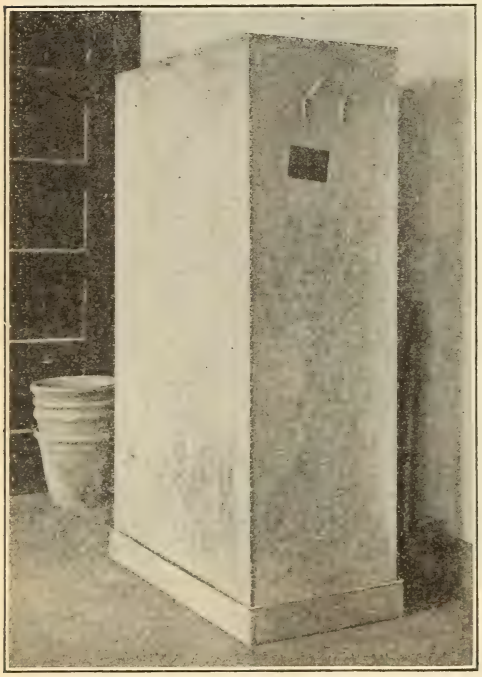


FIG. 2.—Glass-topped galvanized-iron moist chamber used for mature plants.

The incubation period for the two rusts was approximately the same. Generally, though not always, the uredinia of the stem rust appeared first. Cool temperatures seemed to lengthen the incubation period, for during November the house was cooler than during the succeeding months and the uredinia during this time were noticeably slower in appearing. Other factors, such as light, also may have affected the results.

Notes on the appearance of flecks usually were made in 7 to 9 days, and those on the formation of uredinia after a period of not longer than 12 days. Further notes usually were taken on the quantity and character of infection. No counts of uredinia were made; nor should too much emphasis be placed on whether or not all the leaves inoculated were equally infected, for it is obviously impossible to be cer-

tain that the same number of spores was applied in each case. The time of appearance, size of uredinia, and character of infection are deemed of greater importance.

The seedling plants were discarded as soon as final notes were obtained. Those in the series inoculated at the time of heading were allowed to mature in order to obtain herbarium specimens and seed for further work.

SOURCES OF MATERIAL.

The seed of all the varieties tested except Early Ripe[1] was obtained from the 1915 crop grown in rod rows in the rust nursery at Ames, Iowa. Most of these varieties were secured from Mr. C. W. Warburton, of the Office of Cereal Investigations, Bureau of Plant Industry; others were obtained from the Minnesota Agricultural Experiment Station. The forms listed under the Latin (specific) names (greenhouse Nos. 265 to 303) were obtained from Director Bubak, of the botanic garden at Tabor, Bohemia, through Prof. G. M. Reed, of the University of Missouri.

None of these varieties may properly be called a pure line, although some of these rows are traceable (several seasons back) to single plants. Others represent bulk material from rod rows, field plats, or commercial seed stocks. Some of the foreign material is in great need of more careful classification. Mixtures in the previous handling of both the domestic and foreign material sometimes have occurred, but it may be said safely that a majority of the varieties were true to name and for the most part pure, so that where eight or more seedlings were studied most of them really represented the true type of the variety under the name of which they were grown. In the trials on older plants, however, where only two individuals were studied, slight mixtures of the seed sample were more serious.[2]

EVIDENCES OF RUST RESISTANCE IN CEREALS.

Before proceeding to a detailed description and consideration of the observations made and conclusions drawn it will be well to refer to the observations of earlier workers on rust resistance in cereals.

Cobb (3) described certain wheat varieties which were resistant and mentioned the occurrence of dead areas of host tissue. Marryat (6) also observed these dead areas in immune varieties, and Biffen (1) mentions unopened pustules which shed no spores. Stakman (12) observed similar indications of real resistance on (*a*) seedling leaves of certain wheat varieties and on (*b*) leaves of a wheat susceptible to the stem rust of wheat but inoculated with the stem rust of oats. He states that the more resistant a form proved, the more pronounced was the tendency of the rust to kill small areas of the

[1] Seed of this variety was obtained from Dr. H. H. Love. It is very similar to Burt and perhaps identical with that variety. Evidence tends to show that the origin of the two varieties was the same.

[2] All such instances are indicated in Table I.

leaf and that the pustules developed in these areas were always very small. A further indication of immunity is said to be the fact that in the immune forms the incubation period is longer than in susceptible ones.

In a second paper (13) Stakman reports additional studies of the relation between *Puccinia graminis* and plants highly resistant to its attack. The occurrence of the same characteristic flecks or areas of killed tissue is again reported, but a new term, "hypersensitiveness," is used to describe the phenomenon.

Although no histologic studies have yet been made of the oat material, the external macroscopic evidence is in such close agreement with the observed conditions in wheat that there can be little doubt that a struggle between host and parasite of a very similar nature takes place within the tissues of the resistant oat varieties.

Concerning the indications or signs of resistance which were observed in the present study, it may be well to repeat that they are very similar to those in wheat. They are—

1. The prolonged incubation period.
2. The formation of flecks (yellow areas of dead host tissue).
3. The formation of larger blotches of dead tissue and, in extreme cases, the premature death of the whole seedling leaf.
4. Small uredinia, sometimes not completely or promptly rupturing the epidermis, and in *Puccinia graminis avenae* the formation of purple blotches adjacent to the uredinia.
5. The small number of uredinia (relatively unimportant).
6. The production of normal telia of the crown rust on seedling leaves of varieties which these other criteria indicate are resistant.

So far as known to the writer, the occurrence of telia on young seedling leaves of cereals grown in the greenhouse has not been recorded in literature. Melhus (8) states that in his cultures, which appear to have been on older plants, "teleutospores developed in two to three weeks."

It is certain that in the hundreds of seedlings described as very susceptible in the present experiments telia were not produced on a single one following a normal and abundant production of uredinia. The fungus on these leaves seems to have finished its life cycle under these conditions by producing the uredinia. After having remained a normal green color for some time after the formation of uredinia, the leaf finally dries up. That part of the life cycle so common to the rust fungus when on ripening grain plants in the field is not completed. On the other hand, quite early in the work it was observed that in a comparatively short time telia were present on the leaves of seedlings which gave other evidences of being resistant and on which no normal uredinia had been produced. The spores from these sori appear in every way normal, so far as determined by microscopic observation.

On the upper leaf blades of the plants inoculated at the time of heading, where one would normally expect the ultimate production of telia, the resistant plants seemed to produce them at a remarkably early stage. These early telia were produced, in all cases observed, only on leaves infected with the crown rust. It is the belief of the writer that such a hastening in the completion of the life cycle of the fungus is entirely comparable to the well-known instances in the seed plants of the influence of unfavorable conditions, such as drought, poor soil, and injury, in hastening the period of blooming and the maturing of seed.

The teliospores are to be considered necessarily as the final stage in the year's life cycle of the rust. These spores do not serve to spread the infection during the current season, but provide a means for the reproduction of the disease another season or when conditions are again favorable.

It may be argued that the ability which the fungus in these particular varieties possesses to produce this final spore form is the best possible indication of extreme susceptibility. Nevertheless, it is certainly true that if a variety is able to prevent the formation of the summer-spore stage of the rust, the spread of the disease will be checked in localities where only such varieties are grown.

This unusual occurrence of telia on seedling leaves is thought to be an additional evidence of resistance. It has been used sometimes in making the distinction between resistant and susceptible individual plants. Whether this interpretation is accepted or not, the presence of telia on seedling plants of some and their absence on other strains grown under identical conditions is very good evidence of real differences in the protoplasmic reaction of the two hosts, for the progress of the rust fungus following infection is quite different in the two instances. The same stimuli, whether they are chemical, enzymic, or osmotic, which cause the formation of flecks in some varieties and not in others may exercise a rather direct influence on the ability of the parasite to produce a particular spore form at any given time.

Norton (10) reports the abundant occurrence of aecia of the asparagus rust on plants which were resistant to the uredinial stage of the rust.

Smith (11), in studies of the water relations of asparagus rust, has found that "a very direct relation exists between atmospheric moisture and the prevalence of the several spore forms of the rust," and that "the teleuto stage may occur in asparagus beds little affected by the rust, and apparently not preceded by any trace of the other spore stages." He concludes that "the teleuto stage is then to be regarded as a provision for surviving any condition unfavorable to the fungus, whether of food supply, moisture, temperature, or resistance by the host, without regard to season."

Morgenthaler (9) conducted experiments to determine the effect of various influencing factors on the production of teliospores and found that "the time of appearance of the teleutospore stage is not dependent alone on the season of the year, but may be hastened or retarded by many other influences." He also states—

> It is also true that the chemical constitution of the host may provide conditions either favorable or unfavorable for the nourishment of a particular parasite. There are cases known in which the same rust will produce uredospores copiously on one host and only sparingly on another. There may be in certain host plants substances toxic to the fungus, as tannin, which further influence the nourishment of the parasite, and with it its spore production.
>
> This ability of various conditions to influence teleutospore production may also be regarded as a method of protection which the rusts have against influences which are unfavorable for the normal development of the fungus.

EXPERIMENTAL DATA.

Table I presents the results of all the varietal tests, including inoculations of both rusts made on seedling plants and on the plants at time of heading. The inoculations made were as follows:

Stem rust:	
Seedlings	1,256
Headed plants	260
Crown rust:	
Seedlings	1,480
Headed plants	260
Total	3,256

The varieties are arranged alphabetically by name in Table I, except that those bearing the Latin names under which they were received are placed in a separate list, as are also the varieties of red oats which are derivatives of *Avena sterilis*.

The greenhouse number (column 2), the classification list number (column 3), the Cereal Investigations number (column 4), the Seed and Plant Introduction number (column 5), and the Minnesota Agricultural Experiment Station number (column 6) are included in Table I in order that identification may be more certain. It is thus quite possible to compare the record of any variety in this list with statements made in literature regarding it or with field records.

In columns 7 to 10 of Table I the letter S indicates the undoubted and complete susceptibility of that variety under the conditions of the experiment. A question mark (?), S?, or R? indicates some doubt and the need of further tests, while R + S indicates that both resistant and susceptible plants were observed. The letter R has been used only where normal infection did not occur. In these instances the evidence seemed convincing that plants of the variety when tested in the manner here described prevented the formation of normal uredinia and may therefore be regarded as resistant. In a great

majority of cases all leaves or culms inoculated showed infection (normal uredinia) except in certain varieties where there were very evident signs of resistance and to which attention is directed in the footnotes to Table I.

TABLE I.—*Summary of notes on the rust resistance of oat varieties tested in the greenhouse at Cornell University, Ithaca, N. Y., 1915–16.*

[R.= resistant; S.= susceptible.]

Variety.	Identification numbers.					Crown rust.		Stem rust.		Remarks.
	Greenhouse.	Classification list.	Cereal Investigations.	S. P. I.	Minn. A. E. S.	Seedlings.	Plants at heading time.	Seedlings.	Plants at heading time.	
1	2	3	4	5	6	7	8	9	10	
Common (sativa) varieties:										
Abundance	7	.....	.....	.....	272	S.	S.	S.	S.	
Alberta	94	1797	.....	.....	.....	S.	S.	S.	[1] S.?	
American Banner	9	.....	.....	.....	275	S.	S.	S.	S.	
Archangel	11	.....	.....	.....	280	S.	S.	S.	S.	
Archangel × Early Gothland	23	.....	.....	.....	305	S.	S.	S.	S.	
Banner	39	.....	.....	.....	348	S.	S.	S.	S.	
Bicknell	51	.....	206	.....	.....	S.	S.	S.	[2] R.?	
Big Four	42	.....	.....	.....	354	S.	S.	S.	S.	
Black Anthony	102	1804	.....	.....	.....	S.	S.	S.	S.	
Black Beauty	37	.....	.....	.....	342	S.	S.	S.	S.	
Black Diamond	108	1814	.....	.....	.....	S.	.....	S.	.....	
Black Tartarian	29	.....	.....	.....	.....	S.	S.	S.	S.	
Bumper Crop	91	1791	.....	.....	.....	S.	S.	S.	S.	
Challenge	8	.....	.....	.....	273	S.	S.	S.	S.	
Clydesdale	89	1729	.....	.....	.....	S.	S.	S.	[3] S.?	
Colorado No. 9	33	.....	.....	.....	336	S.	S.	S.	S.	
Conqueror	96	1798	.....	.....	.....	S.	S.	S.	S.	
Culberson selection	68	.....	651	.....	.....	S.	S.	S.	S.	
Danish Giant	69	.....	672	.....	.....	S.	S.	S.	S.	
Early Champion	4	.....	.....	.....	.....	S.	[4] R.?	S.	[5] R.+S.	Mixed seed.
Early Gothland	2	.....	.....	.....	26	S.	[6] S.?	S.	[7] R.?	
English Wonder	104	1807	.....	.....	.....	S.	S.	S.	S.	
Garton No. 5	83	.....	730	.....	.....	S.	S.	S.	S.	
Garton No. 396	46	.....	.....	.....	405	S.	S.	S.	S.	
Goldmine	103	1805	.....	.....	.....	S.	S.	S.	S.	
Green Mountain	97	1799	.....	.....	.....	S.	S.	S.	S.	
Green Russian	41	.....	.....	.....	350	S.	S.	S.	[8] R.+S.	Do.
Johnson	106	1808	.....	.....	.....	S.	S.	S.	S.	
Junghans	98	1800	.....	.....	.....	S.	S.	S.	S.	
King Oscar	36	.....	.....	.....	341	S.	S.	S.	S.	
Ligowo	1	.....	.....	.....	6	S.	S.	S.	S.	
Lincoln	34	.....	.....	.....	340	S.	S.	S.	S.	
Pickett	88	1728	.....	.....	.....	S.	S.	S.	S.	
Roosevelt	43	.....	.....	.....	391	S.	S.	S.	S.	
Ruakura Rustproof [9]	79	.....	701	.....	.....	[10] R. (+S.)	[11] R.+	[12] S.?	[13] R. +S.	Do.

[1] Normal infection on one plant; on the other, only a few uredinia surrounded by purple blotches.
[2] Only a few abnormally small uredinia in 14 days after inoculation.
[3] No uredinia in 10 days after inoculation, and finally only one on each culm, accompanied by purple color of host tissue.
[4] Only a few tiny uredinia on each leaf.
[5] Normal uredinia on one culm; only a few on the other.
[6] Infection only fairly vigorous.
[7] Unusually small uredinia first appeared 14 days after inoculation.
[8] Normal infection on one culm; no uredinia on the other.
[9] The results with this variety probably were more interesting and valuable than those from any other included in the test, for there were signs of resistance to both rusts at both stages of growth. This variety is of undoubted value as a source of the character of rust resistance, the more so because of its resemblance to yellow and white oat varieties of the *Avena sativa* group.
[10] Six leaves severely rusted; on four only extremely small uredinia. In two pots of seedlings later inoculated no normal infection resulted.
[11] Flecks only; no uredinia. Within two weeks the small dark telia, characteristic of resistant varieties, were formed.
[12] Uredinia moderately abundant, somewhat small and surrounded by yellow flecks.
[13] On one plant uredinia were abundant and of normal size. On the other plant they were small and tardy in breaking through the epidermis.

TABLE I.—*Summary of notes on the rust resistance of oat varieties tested in the greenhouse at Cornell University, Ithaca, N. Y., 1915–16*—Continued.

[R.= resistant; S.= susceptible.]

Variety.	Identification numbers.					Crown rust.		Stem rust.		Remarks.
	Greenhouse.	Classification list.	Cereal Investigations.	S. P. I.	Minn. A. E. S.	Seedlings.	Plants at heading time.	Seedlings.	Plants at heading time.	
1	2	3	4	5	6	7	8	9	10	
Common (sativa) varieties—Continued.										
Scottish Chief	92	1793				S.	S.	S.	S.	
Sensation	107	1811				S.	S.	S.	S.	
Shadeland Challenge	71		680			S.	S.	S.	S.	
Shadeland Climax	72		681			S.	S.	S.	S.	
Shireff	12				285	S.	S.	S.	S.	
Siberian	13				286	S.	S.	S.	S.	
Sixty-Day (Minn.)	3				261	S.	S.	S.	S.	
Sixty-Day (parent)						S.	S.	S.	S.	
Storm King	99	1802				S.	S.	S.	[14] S.?	
Stube	87	1726				S.	S.	S.	S.	
Swedish Select	6				271	S.	S.	S.	S.	
White Bonanza	44				403	S.	S.	S.	S.	
White Russian	18				301	S.	S.	S.	S.	
White Tartarian (check)	5					S.	S.	[15] S.?	R.	
White Tartarian	101	1803					S.		[16] S.?	
White Wonder	17				299	S.	S.	S.	S.	
Unnamed	64		605				[17] S.?		S.	
Do	117		609	25259		S.	[18] S.?	S.	S.	
Avena sativa (botanical races):										
Avena sativa	120			25356		S.	S.	S.	S.	
A. s. montana	265					S.	S.	S.	S.	
A. s. krausei	266					S.	S.	S.	S.	
A. s. aurea	267					S.	S.	S.	S.	
A. s. nigra	274					[19] S.?	S.	S.	S.	
A. s. setosa	275					[20] S.?	S.	S.	S.	
A. s. aristata	276					S.	S.	S.	S.	
A. s. mutica	277					S.	S.	S.	S.	
Do	278					S.	S.	S.	S.	
Do	279					S.	S.	S.	S.	
Do	280					S.	S.	S.	S.	
Do	281					S.	S.	S.	S.	
Do	282					S.	S.	S.	S.	
Do	283					S.	S.	S.	S.	
Do	284					S.	S.	S.	S.	
Do	285					S.	[21] R.?	S.	S.	
Do	286					S.	S.	S.	S.	
Do	287					S.	S.	S.	S.	
Do	288					S.	S.	S.	S.	
Do	289					S.	S.	S.	S.	
Do	290					S.	S.	S.	S.	
A. s. praegravis	291					S.	S.	S.	S.	
Do	292					[22] R.?	S.	S.	[23] R.?+S.	
Do	293					S.	S.	S.	S.	

[14] Normal uredinia in the usual time on one plant; on the other culm subepidermal uredinia, at first small and surrounded by spots of purple color, but later rupturing the epidermis and attaining normal size.

[15] Uredinia usually numerous, but small. Epidermis not always ruptured early; on some plants only flecks with tiny uredinia were formed.

[16] Few uredinia, normal in size but accompanied by blotches of purple color, probably an anthocyanin, similar in appearance to those commonly present on sorghum and maize plants. These blotches were often observed adjacent to stem-rust uredinia and may indicate an unusual disturbance in the physiologic activities of the host cells, whether or not they are directly related to the question of resistance.

[17] Light infection; uredinia few and of small size.

[18] Light infection; uredinia tardy in appearing and never reaching normal size.

[19] Normal infection on five leaves; light infection on two leaves.

[20] Normal infection on six leaves, medium on two, and only a light infection on two.

[21] Only a very few tiny uredinia, formed 14 days after inoculation.

[22] No uredinia on leaves of first seedlings inoculated; the leaves appeared dry and dead within a few days after inoculation. In the second series inoculated, only one leaf was severely infected. Eight showed medium infection, and on one no uredinia appeared.

[23] Normal infection on one plant; no indication of infection on the other.

TABLE I.—*Summary of notes on the rust resistance of oat varieties tested in the greenhouse at Cornell University, Ithaca, N. Y., 1915–16*—Continued.

[R.= resistant; S.= susceptible.]

Variety.	Identification numbers.					Crown rust.		Stem rust.		Remarks.
	Greenhouse.	Classification list.	Cereal Investigations.	S. P. I.	Minn. A. E. S.	Seedlings.	Plants at heading time.	Seedlings.	Plants at heading time.	
1	2	3	4	5	6	7	8	9	10	
Avena sativa (botanical races)—Continued.										
A. s. trisperma	294					[24] R.?	[25] R.?	S.	S.	
A. s. brunnea	297					S.	S.	S.	S.	
A. s. mutica	298					S.	S.	S.	S.	
A. s. praegravis	299					S.	S.	S.	S.	Mixed seed.
A. s. mutica	301					S.	S.	S.	S.	
Do	302					S.	S.	S.	S.	
Do	303					S.	[26] R.?	S.	S.	
Miscellaneous species of Avena:										
Avena barbata	119			25354		[27] S.?	[28] R.?+S.	S.	S.	
A. brevis	112					S.	S.	S.	S.	
Do	295					[29] S.?	[30] R.?	S.	S.	
A. fatua	109						S.		S.	Do.
A. f. glabrata	111					S.	S.	S.	S.	
A. ludoviciana	114					S.	S.	S.	S.	
A. nuda	118			25351		S.	S.	S.	S.	
Do	126			16894		S.	S.	S.	[31] R.?	Do.
A. orientalis pugnax	268					S.	S.	S.	S.	
A. o. tristis	269					S.	S.	S.	S.	
A. o. tartarica	270					S.	S.	S.	S.	
A. o. mutica	271					S.	S.	S.	[32] R.?	
A. o. flava	272					S.	S.	S.	S.	
A. o. obtusata	273					S.	[33] R.?	S.	S.	
A. purpurea	121			25357		S.	S.	S.	[34] R.?	Do.
Avena sterilis and varieties:										
Avena sterilis	116		543	21751		S.	[35] S.?	S.	S.	
Do	296					S.	S.	S.	S.	
Algerian Red	47					S.	S.	S.	S.	
Appler	74		695			[36] R.?	R.	S.	S.	
Burt	48					[37] S.?	[38] R.	S.	S.	

[24] In the first series inoculated, small uredinia on two out of nine leaves, flecks only on seven. All leaves soon dry and dead. In the second series inoculated, heavy infection occurred on five and light infection on five.

[25] Flecks only 10 days after inoculation; later a few tiny uredinia, accompanied and surrounded by many flecks.

[26] No uredinia 10 days after inoculation; later a few tiny ones on each leaf, surrounded by flecked areas of host tissue.

[27] In the first series fairly heavy infections were obtained on all leaves inoculated, but uredinia were small. In the second series normal infection on two leaves, medium on eight, and light on two.

[28] Heavy infection on only one leaf; only a few tiny uredinia on the other two.

[29] In the first series of inoculations fairly vigorous infections were obtained on some of the leaves. On other leaves only a few small uredinia appeared, the leaf soon drying and turning brown. In a second series, normal infection occurred on all leaves inoculated.

[30] Flecks only 10 days after inoculation. A few small uredinia appeared later, accompanied by distinct flecks.

[31] On one plant, uredinia nearly normal in size, but accompanied by purple blotches; no uredinia were produced on the other plant.

[32] Uredinia few and small; infection not heavy.

[33] No evidence of infection in 10 days after inoculation; the few uredinia finally produced were small.

[34] Uredinia normal on one plant; on the other small and surrounded by purple blotches.

[35] Flecks only on one of the two leaves inoculated. The leaf soon dried up. A large number of normal uredinia appeared on the tip of the other leaf. On most of the leaf surface, however, there were very few uredinia but many flecks.

[36] Of the first series of 11 leaves inoculated 5 were heavily infected, while on 6 only flecks were evident. In the second series inoculated uredinia were produced on all leaves but were accompanied by many yellowish flecks, and larger blotches of dead host tissue surrounded each uredinium.

[37] In the first series of leaves inoculated 6 out of 10 leaves were rather heavily rusted, 1 showed light infection, and on 3 only flecks appeared. In the second series nearly normal infections were secured on all the 8 leaves inoculated. In the third series medium to good infection resulted on all 11 leaves inoculated. Many of the uredinia were of normal size, but surrounded by light yellowish green flecks.

[38] No uredinia. Rather indistinct light-green flecks were observed, indicative of the presence of rust hyphæ.

TABLE I.—*Summary of notes on the rust resistance of oat varieties tested in the greenhouse at Cornell University, Ithaca, N. Y., 1915–16*—Continued.

[R.= resistant; S.= susceptible.]

Variety.	Identification numbers.					Crown rust.		Stem rust.		Remarks.
	Greenhouse.	Classification list.	Cereal Investigations.	S. P. I.	Minn. A. E. S.	Seedlings.	Plants at heading time.	Seedlings.	Plants at heading time.	
1	2	3	4	5	6	7	8	9	10	
Avena sterilis and varieties—Continued.										
Burt	76	.....	696	....	.....	[39] R.?	[40] R.	S.	S.	
Do	81	.....	710	....	.....	[41] R.	[42] R.?	S.	S.	
Early Ripe	.....	.....	.....	....	.....	[43] R.(+S)	[44] R.	S.	S.	
Cook	77	.....	697	....	.....	[45] R.?	[46] R.	S.	S.	
Fulghum	73	.....	694	....	.....	[47] S.?	[48] R.	S.	S.	
Golden Rustproof	61	.....	509	....	.....	[49] S.?	[50] R.?	S.	S.	
Do	93	1796	.....	....	.....	S.	S.	S.	S.	
Italian Rustproof	54	.....	388	....	.....	S.	S.	S.	[51] S.?	
Do	57	.....	397	....	.....	S.	S.	S.	S.	
Italian Rustproof selection.	58	.....	409–4	....	.....	[52] R.	[53] R	S.	S.	
Red Rustproof	24	.....	.....	....	309	S.	S.	S.	S.	
Red Rustproof selection	52	.....	261–7	....	.....	[54] S.?	S.	S.	[55] R.+S.	
Do	62	.....	518–15	....	.....	[56] R.?	[57] R.	S.	S.	
Do	78	.....	700	....	.....	[58] S.?	S.	S.	S.	
Siberian Red	59	.....	487	....	.....	S.	S.	S.	[59] R.?	
Turkish Rustproof selection.	53	.....	356–19	....	.....	S.	S.	S.	S.	
Do	67	.....	627	....	.....	[60] R.?	[61] R.	S.	S.	

[39] Three series of inoculations were made. In each some leaves were rather heavily rusted, others lightly, and on some no uredinia (only flecks) were formed. Telia were freely produced on leaves where no normal uredinia had previously ruptured the epidermis.

[40] Normal uredinia on one leaf; flecks only on the other.

[41] In the three series of inoculations made no leaf was heavily rusted. Only a few had even a slight infection, while most of them very quickly showed large reddish brown blotches of dead tissue and smaller yellowish green flecks and no uredinia (see Pl. III).

[42] Normal infection at the base of each leaf, the upper portion heavily flecked and soon turning brown in color, with no normal uredinia.

[43] In the seven series inoculated, there were both susceptible and resistant plants, the former with many normal uredinia, the latter with few and small uredinia or flecks only. On many leaves, large blotches of host tissue were killed soon after inoculation. On some of these, telia were later developed.

[44] Of five leaves inoculated, on only one were normal uredinia produced and these only at the base. On one leaf a few tiny uredinia were formed, and on three flecks only appeared.

[45] In the first series of 6 leaves inoculated, a few light-green flecks furnished the only evidences of infection. In two later series of 6 and 10 leaves inoculated, normal infections occurred on 8 of the 16, while the other 8 had only small uredinia or flecks.

[46] No uredinia appeared in three weeks after inoculation; then only tiny ones on one leaf. Distinct flecks were evident.

[47] Of 9 leaves in the first series inoculated, 1 was heavily rusted, 6 medium, and on 2 only flecks appeared. Of 14 leaves in a second series, fairly normal infection occurred on all, though some uredinia were rather small. No sharp indications of resistance.

[48] Two leaves inoculated; on neither were any normal uredinia produced. Uredinia small and accompanied by flecks.

[49] In the first series of 8 leaves, normal infection occurred on 5, light on 2, flecks only on 1. In the second series of 9 leaves, 4 were heavily rusted and 5 lightly.

[50] No uredinia in 11 days after inoculation, then only 1 or 2 small ones on each leaf. There were also blotches of dead host tissue.

[51] No uredinia normal in size or vigor; after 21 days they were still small.

[52] Of 6 inoculated leaves in the first series, normal infection was produced on 3 and very small uredinia and flecks on 3. No normal infection occurred on 9 leaves inoculated in the second series. There were only a few tiny uredinia with many flecks.

[53] No signs of infection except dead leaf tips.

[54] In the first series of 9 leaves inoculated, normal infection was secured on 6, while only flecks appeared on 3 in the time characteristic for uredinia. Telia were formed later. In the second series, the 2 leaves inoculated were rusted heavily.

[55] Normal (very heavy) infection on one culm; only a very few small uredinia on the other.

[56] No evidences of infection on the leaves of the first series inoculated. Only a few tiny uredinia were formed on the 9 leaves in the second series inoculated.

[57] Only a few very small uredinia; many flecks.

[58] Of 10 leaves in the first series inoculated, 6 were heavily rusted and a light infection on 4. Of 11 leaves in the second series, 6 were heavily rusted, on 4 only a few very small uredinia developed, and on 1 only flecks appeared in the time usual for uredinia formation. An abundance of telia later occurred.

[59] No uredinia of normal size and vigor; only a few tiny ones on each leaf.

[60] Of the first series of five leaves inoculated, one was very heavily rusted, three had only a light infection, and on one only flecks were produced. All leaves of the second series inoculated were rather heavily rusted, but numerous flecks were observed, also indicating some degree of resistance.

[61] Infection not heavy; uredinia on each leaf few and small.

DISCUSSION OF RESULTS.

The notes in Table I on the varieties which showed resistance to one or both rusts indicate that rust resistance is very specific and that a particular variety may be entirely susceptible to one rust and somewhat resistant to the attacks of another.[1]

Of the 122 strains tested, 80 unquestionably were susceptible to both rusts in both stages of growth. This does not imply that these varieties are not of great commercial value in other respects and is not sufficient reason for discarding them from cultivation, for at present there are no suitable varieties to substitute for the best of them. It probably does remove them, however, from the list which is to afford promise of rust-resistant varieties. Heavy infections were obtained on practically all of these, and at least some normal uredinia were formed on all. While such greenhouse tests do not represent field conditions accurately, the optimum conditions for infection provided should make the evidences of resistance which appeared in some varieties all the more valuable. Some of these varieties may show some resistance under field conditions and some of them have properly been recommended as rust-escaping because of their early-ripening habit, as, for instance, the Sixty-Day and Kherson varieties.

In 80 out of the 122 cases the results at two distinct periods in the life of the host plant have led to identical conclusions as to the susceptibility of the variety. In some of the resistant varieties, also, both seedlings and mature plants gave the same evidences of resistance, though the results are not always in agreement. These susceptible varieties need not be discussed in further detail, but the list includes the following commonly grown sorts: American Banner, Big Four, Ligowo, Lincoln, Siberian, Sixty-Day, Swedish Select, and White Russian. In this list are included also most of the botanical species represented and nearly all of the recently introduced foreign varieties.

In the *Avena sterilis* group also, where most of the resistance to crown rust is found, several strains are very susceptible to the crown rust, as, for instance, Greenhouse No. 296, Red Algerian, and one strain each of Golden Rustproof, Italian Rustproof, Red Rustproof, and Turkish Rustproof.

Not all varieties of the *Avena sterilis* group show perceptible resistance to either rust, and great care should be exercised in recommending to farmers these or other varieties as rust resistant. Still greater care is necessary in choosing a strain to use as a parent

[1] The studies of these varieties indicate the necessity for selecting and working from individual plants, for certainly within the same variety, and even within a line supposed to be pure for other characters, differences of a major degree in rust resistance exist.

variety with the purpose of obtaining a resistant variety through hybridization.

None of the seedlings of the 23 varieties belonging to the *Avena sterilis* group showed any resistance to the stem rust, and in only three of the varieties did the plants inoculated at heading time give any evidence of resistance to this rust. It is entirely safe to conclude that all of these varieties are quite susceptible to stem rust, and the *Avena sterilis* group probably will offer little in the way of resistance to stem rust that is of value to the plant breeder.

Of these 23 varieties 16 show some degree of resistance to crown rust. Certain strains were strikingly resistant in both the seedling stage and at heading time, and from the clear-cut evidences of resistance there can be no doubt of the presence of resistance to crown rust in varieties of this group.

These varieties which are actually resistant to crown rust, if found to be high in yield, should replace some of the "rustproof" types now being grown in the Southern States. They may be of use also in the breeding of rust-resistant varieties for culture in other sections of the country.

Table I shows that there are many more cases of resistance to the crown rust than to the stem rust. This is especially true of the work on seedlings, where none of the varieties tested except White Tartarian and Ruakura Rustproof showed any resistance to stem rust.

In the studies of both rusts, more apparent cases of resistance are recorded from the inoculations made on the plants at the time of heading. This may be due to the fact that plants are more susceptible as seedlings than when more mature. It is more likely, however, that some of the failures to get normal or heavy infection were due to the fact that it was more difficult to wet thoroughly, and hence inoculate heavily, the upper leaf blades and sheaths than the young seedling leaves.

The use of the word "immune" is avoided, for in the forms studied none were observed in which very distinct evidences of infection did not appear. The words "resistant" and "resistance" are used only in a relative sense and refer to that condition in which normal urediniospore production by the fungus was either prevented or seriously interfered with. As Stakman (13) has pointed out, the quality which is called resistance may actually be, in the extreme sense, susceptibility or hypersensitiveness. It amounts to "commercial resistance," using that expression to describe a variety which will suffer less severe damage in the field than some others.

SUMMARY AND CONCLUSIONS.

(1) Two distinct rusts of oats are common in the United States: (*a*) Stem rust, *Puccinia graminis avenae* Erikss. and Henn., and (*b*)

crown or leaf rust, *Puccinia lolii avenae* McAlpine. The stem rust is more common in the North, while the crown rust, though practically always present, seems to be most abundant and serious in the South.

(2) Greenhouse studies are of value in determining varietal resistance under optimum conditions for infection. These studies, however, should always be supplemented by rust nursery and field trials.

(3) Plants of more than 120 strains of oats were inoculated at two different periods of growth (the seedling stage and the heading stage) and their reaction to both rusts determined.

(4) The inoculations made on these varieties were as follows: Stem rust.—Seedlings, 1,256; headed plants, 260. Crown rust.—Seedlings, 1,480; headed plants, 260. Total, 3,256.

(5) Of more than 120 strains tested, 80 were found to be entirely susceptible to both rusts at both stages of growth. Unquestionable resistance to stem rust was present in only two varieties, White Tartarian and Ruakura Rustproof. Several varieties of the red-oat group (*Avena sterilis*), including certain strains of Burt, Cook, Appler, Italian Rustproof, Red Rustproof, and Turkish Rustproof, are very resistant to the crown rust. Ruakura Rustproof and certain recently introduced species of Avena also gave indications of resistance to crown rust.

(6) Rust resistance is shown to be specific, for many of the varieties which are resistant to crown rust are thoroughly susceptible to the stem rust under identical conditions. The evidences of resistance described for wheat are shown to apply also to resistant oat varieties. In addition, the early production of telia on seedling leaves has been observed and is believed to be an indication of resistance.

(7) Further search must be made for varieties resistant to stem rust.

(8) Varieties of the *Avena sterilis* group which are really resistant to the crown rust, if found to be high in yield, should replace other "rustproof" varieties now being grown in the Southern States. None of the varieties of this group which have been tested will withstand the attacks of stem rust.

(9) A basis is now offered for making selections and crosses to produce improved oat varieties resistant to crown rust and suitable for culture in the several oat-growing areas of the United States.

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